Hemispheric asymmetries for whole-based and part-based faceprocessing in the human brain

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Hemispheric Asymmetries for Whole-Based and Part-Based Face Processing in the Human Fusiform Gyrus

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Abstract

■ Behavioral studies indicate a right hemisphere advantage for processing a face as a whole and a left hemisphere superiority for processing based on face features. The present PET study identifies the anatomical localization of these effects in well-defined regions of the middle fusiform gyri of both hemispheres. The right middle fusiform gyrus, previously described as a face-specific region, was found to be more activated when matching whole faces than face parts whereas this pattern of activity was reversed in the left homologous region. These lateralized differences appeared to be specific to faces since control objects processed either as wholes or parts did not induce any change of activity within these regions. This double dissociation between two modes of face processing brings new evidence regarding the lateralized localization of face individualization mechanisms in the human brain. ■

INTRODUCTION

Human face recognition is a complex function that may rely on specific neural regions of the brain, as suggested by behavioral, neuropsychological, cellular recordings, and more recently neuroimaging studies (reviewed in Tovée, 1998). Regions of the human brain responding specifically to human faces have recently been evidenced by neuroimaging studies (Dubois et al., 1999; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999b; Halgren et al., 1999; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997; Puce, Allison, Gore, & McCarthy, 1995; Haxby et al., 1994, Haxby et al., 1999; Sergent, Otha, & McDonald, 1992). Among the studies where low-level visual features of faces and objects were controlled, and other factors such as intracategorical discrimination, some have disclosed either bilateral face-specific activity in regions of the middle fusiform (Gauthier et al., in press, Gauthier et al., 1999b; Halgren et al., 1999; Haxby et al., 1999; Ishai et al., 1999) or differences between faces and objects mainly in the right hemisphere fusiform gyrus (Kanwisher et al., 1997; McCarthy et al., 1997). These findings are consistent with lesion studies illustrating that most cases of prosopagnosia, i.e., the inability to recognize faces following a brain lesion, are due to bilateral damage to the occipito-temporal cortex, although there are several case descriptions of unilateral right-sided lesions (Michel, Poncet, & Signoret, 1989; Landis, Regard, Bliestle, & Kleihues, 1988; De Renzi, 1986; but see also Ettlin et al., 1992). The necessary involvement of the left hemisphere in prosopagnosia is still a matter of debate but the dominant view among neuropsychologists (Farah, 1990; Moscovitch, Winocur, & Behrmann, 1997) and cognitive neuroscientists (e.g., McCarthy et al., 1997) is that right hemisphere fusiform regions are specifically involved in face processing while left fusiform regions are part of a more general, i.e., bilateral, object recognition system. However, there is also considerable behavioral and neuropsychological evidence suggesting that the right and left hemispheres are *both* involved in face processing but in different ways. Faces presented in the usual upright orientation to the left visual field are identified more rapidly and more accurately than when they are presented in the right visual

field (Rhodes, 1993; Hillger & Koenig, 1991; Levine, Banich, & Koch-Weser, 1988; Leehey, Carey, Diamond, & Cahn, 1978). Inverting faces, which disrupts configural[1] coding of faces (e.g., de Gelder & Rouw, in press; Rhodes, Brake, & Atkinson, 1993; Tanaka & Farah, 1993), eliminates or reduces the right hemisphere advantage for faces (Hillger & Koenig, 1991; Leehey et al., 1978). This observation suggests that the right hemisphere tends to process an overall representation of the face whereas the left hemisphere relies more on a feature-detection strategy. In addition, tachistoscopic studies have also demonstrated left-hemisphere superiority when feature-by-feature processing of faces is induced by task manipulation (Hillger & Koenig, 1991). These behavioral findings are consistent with neuropsychological observations providing indirect evidence that the configural coding mechanisms used for faces are lateralized to the right hemisphere since right brain injured patients are no longer better at matching normal than inverted faces (Yin, 1970).

In the light of such findings, one may understand why neuroimaging studies have so far either revealed right hemisphere face-specific activation or bilateral activity increase in the middle fusiform regions when face perception is compared to object perception. Face-specific activity has been mostly observed in passive stimulation paradigms (Halgren et al., 1999; Kanwisher et al., 1997; McCarthy et al., 1997; Puce et al., 1995) or 1-back recognition tasks (Kanwisher et al., 1997). In addition to leaving the precise function of the face-specific areas unclear (Tovée, 1998), these paradigms may have obscured the role of the left hemisphere in face processing since they may rely heavily on configural mechanisms lateralized to the right hemisphere (Rhodes, 1993).

The present PET study was designed to test this specific possibility. The first goal was to clarify the role of the middle fusiform regions in face-specific processing, and second to provide evidence that the right fusiform regions are more involved in face-specific processing when the whole face is processed than when subjects are engaged in a task that requires an analysis of the face based on individual parts.

Normal subjects were scanned while they were presented either with control photographs of objects and

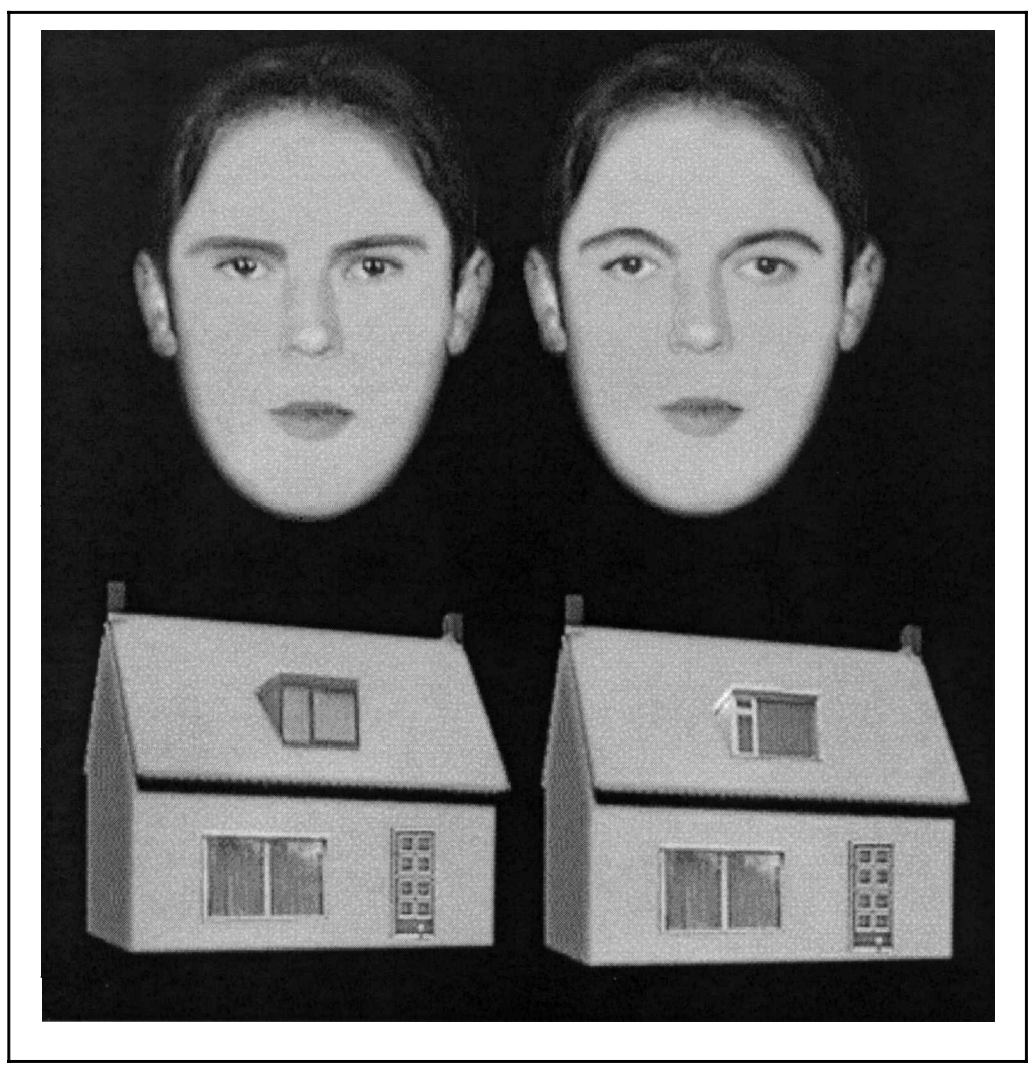

Figure 1. Examples of stimuli used in the experiment. The two faces presented above differ only by the eyes, while the two instances of houses differ by the superior window.

faces (scans 1, 2, 11, and 12), or photograph-like quality pictures of houses and faces (scans 3 to 8, experimental conditions). Houses were chosen as control stimuli because, like faces, members of that category have a canonical orientation, they tend to share a common configuration and they have the same kinds of parts. Houses were also used in previous behavioral (de Gelder & Rouw, in press; Donnelly & Davidoff, 1999; Tanaka & Farah, 1993) and neuroimaging (e.g., Haxby et al., 1999; Kanwisher et al., 1997) experiments as control objects for faces. The control scans were added to allow a better identification of face-selective regions, and also to ensure that the face-specific regions identified were not observed due to particular differences between faces and houses. During these control scans, subjects were presented either with objects of various categories or with faces and had to perform a delayed matching task (see Methods) on these stimuli. In the experimental tasks, identical images were presented under two different instruction conditions (see Figure 1). In the WHOLES conditions subjects had to match two whole stimuli, whole faces (FW) or houses (HW). The same stimuli were used for the PARTS conditions where the task was to match either the eyes or the mouth of the face (FP), or a large window or a smaller one, for the house (HP). Before each scan, subjects were instructed which feature they had to match and were presented with a few trials.

Based on recent suggestions (Tovée, 1998) and on a previous PET study conducted in our laboratory (Dubois et al., 1999), we expected to find a common network of fusiform regions associated with face processing among which should be the previously described face fusiform area (FFA, see Kanwisher et al., 1997) in the right middle fusiform gyrus, and a homologous region in the left fusiform gyrus (Dubois et al., 1999; Gauthier et al., 1999b, Gauthier, Kanwisher, Anderson, Skudlarski, & Gore, 1999a; Haxby et al., 1999). Assuming that the FFA is involved in recognizing individual faces, a function that normally requires a configural processing of the face, it was expected that processing whole faces would lead to greater activity within this right hemisphere region than would processing face parts. Regarding the left middle fusiform region, the difference between face and objects was expected to be less, as has been described in previous studies (Dubois et al., 1999; Gauthier et al., 1999b; Haxby et al., 1999; Kanwisher et al., 1997). Assuming that recognition by the left side of the brain may occur by piecemeal processing of face features rather than of the whole image as a single configuration (Tovée, 1998), we also hypothesized a larger activation for the part-based face processing over the whole one in the left fusiform region, although usually the advantage of the left hemisphere for part-based processing is less clear than the superiority of the right hemisphere for configural processing (for recent fMRI studies see Martinez et al., 1998 and for behavioral studies with divided field presentation see Hillger & Koenig, 1991). Our predictions for houses were less firm because the role of configuration in the perception of objects is unclear (see Donnelly & Davidoff, 1999 as well as Tanaka & Farah, 1993) and also because we search for task modulations within face-selective regions and not object-selective regions.

RESULTS

Our behavioral results (Table 1) are consistent with studies showing better performance for processing whole faces rather than face parts presented in whole faces (Tanaka & Farah, 1993). Interestingly, the opposite is observed for the houses. A two-way repeated-measures ANOVA by subject for the reaction times (RTs) showed a significant processing (whole vs. parts) by stimulus interaction: ($F(1, 7) = 13.6$; $p < .01$) (all other Fs < 1). Three-way repeated-measures ANOVA by subject for the accuracy rates did not show any significant effect. A paired t test between the baseline conditions did not show any significant difference for RTs ($p = .212$).

We localized the brain areas more involved in face than object processing ($Z > 3.09$; $p < .001$, uncorrected for multiple comparisons) by subtracting the activations obtained when subjects viewed objects, including houses, from that obtained when viewing all kinds of

Table 1. Behavioral Data

	Reaction time (msec)		*Accuracy (% correct)*	
	Mean	*SD*	*Mean*	*SD*
Face processing (W)	938	182	90	5
Face processing (P)	1028	199	88	7.5
House processing (W)	1033	187	91	11
House processing (P)	926	199	95	4.5
Baseline faces	825	195	96	4.4
Baseline objects	773	200	96	3.5

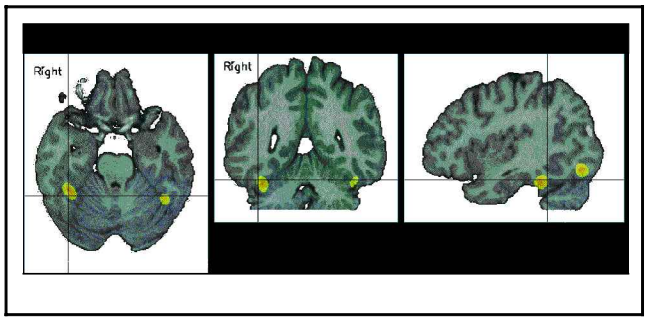

Figure 2. Functionally different face-specific regions in the human brain. Axial, coronal and sagittal sections through a subject's normalized MRI scan are shown. The transverse (left) and sagittal slices show the right and left middle face-specific fusiform regions, which are differentially activated by processing wholes or parts of faces. The coronal slice (right) show the right-hemisphere view with functional regions rFFA and LO.

faces (localizer contrast or main effect). This comparison revealed bilateral activation in the middle fusiform gyrus (right: 38, – 44, – 26; left: – 42, – 50, – 26; BAs37; see Figure 2) and in the right posterior-lateral fusiform region (BA19, 46 – 76 – 14).[2] These regions (Figure 2) are consistent with the brain areas associated with face processing in numerous previous PET and fMRI studies and correspond to the so-defined common face-processing network that we recently described with the same PET device (Dubois et al., 1999). The lateral right posterior fusiform gyrus corresponds anatomically to the lateral-occipital (LO) complex which was found to be activated by objects of all kinds, familiar and unfamiliar, without any clear selectivity for the type of item (Grill-Spector et al., 1998; Malach et al., 1995). However, weak face-specific activity has also been evidenced in the LO when compared to visual patterns (Dubois et al., 1999), textures and letters (Puce et al., 1995), objects and cars (Halgren et al., 1999), or in a few right-handed subjects (4/10) (Kanwisher et al., 1997) when faces were compared to canonical views of familiar objects such as a spoon, a lion, or a car.

The localization (38, – 44, – 26) of the maxima in the right middle fusiform face-specific region in the present study is near the FFA, as described in the original study (Kanwisher et al., 1997: 40x, – 55y, – 10z), and in other fMRI and PET studies (Dubois et al., 1999; Halgren et al., 1999; McCarthy et al., 1997; Clark, Keil, Maisog, Courtney, Ungerleider, & Haxby, 1996, Clark, Maisog, & Haxby, 1998; Puce et al., 1995; Haxby et al., 1994). The third face-selective area observed in the present study is smaller in functional size (77 voxels above threshold, see Table 2). This region is homologous to the right middle fusiform face area and has been described as face-specific or at least face-sensitive in many previous neuroimaging studies (Dubois et al., 1999; Gauthier et al., 1999b; Halgren et al., 1999; Haxby et al., 1999; Puce et al., 1995; six subjects in Kanwisher et al., 1997). To avoid confusion, and because our experiment indicates that they do not engage identical face-selective mechanisms, these two middle fusiform regions are referred to as r(ight)FFA and l(eft)FFA in the present study.

We next examined the functional modulations induced by processing wholes or parts of the stimuli within these rFFA, lFFA, and LO by means of a masking procedure (Dubois et al., 1999; George et al., 1999). As activation was tested in the areas implicated by the main effect only, no correction for multiple comparisons was used and the threshold of significance was set at $p < .05$, uncorrected (Dubois et al., 1999; Fink et al., 1996). Confirming our hypothesis, the rFFA was found to be more activated for FW than FP ($Z = 2.34$; 62 contiguous voxels at $p < .05$). The percentage of blood-flow increase in FW as compared to FP in a 3-mm radius spherical region, with 38, – 44, – 26 as spherical center, was 1.56% (1.65% for voxel 38, – 44, – 26), indicating that the right middle fusiform gyrus was more involved in processing whole faces than in processing face parts. This task modulation was specific to faces since comparing processing of whole houses or house parts did not yield any significant difference (see Figure 3). A double dissociation[3] between whole- and part-based processing of faces regarding hemispheric specialization was evidenced since the left homologous fusiform region (lFFA) was more activated for FP than FW ($Z = 1.76$, 13 contiguous voxels at $p < .05$). The percentage of blood-flow increase in FP as compared to FW in a 3-mm radius spherical region with – 42, – 50,

Table 2. Relative Increases in Brain Activity Associated with Face Processing as Compared with Visual Object Processing ($p < .001$, Uncorrected for Multiple Comparisons)

		Coordinates				
Region	*Side*	*x*	*y*	*z*	*Z score*	*Voxel size*
Middle fusiform gyrus (rFFA)	R	38	– 44	– 26	4.23	206
Middle fusiform gyrus (lFFA)	L	– 42	– 50	– 26	3.73	77
Posterior fusiform gyrus	R	46	– 76	– 14	4.43	207

Coordinates (in standard stereotaxic space; Talairach & Tournoux, 1988) refer to maximally activated foci as indicated by the highest Z score within an area of activation. x = distance (mm) to right (+) or left (–) of the midsagittal line; y = distance anterior (+) or posterior (–) to the vertical plane through the anterior commissure; z = distance above (+) or below (–) the bicommissural (AC–PC) line.

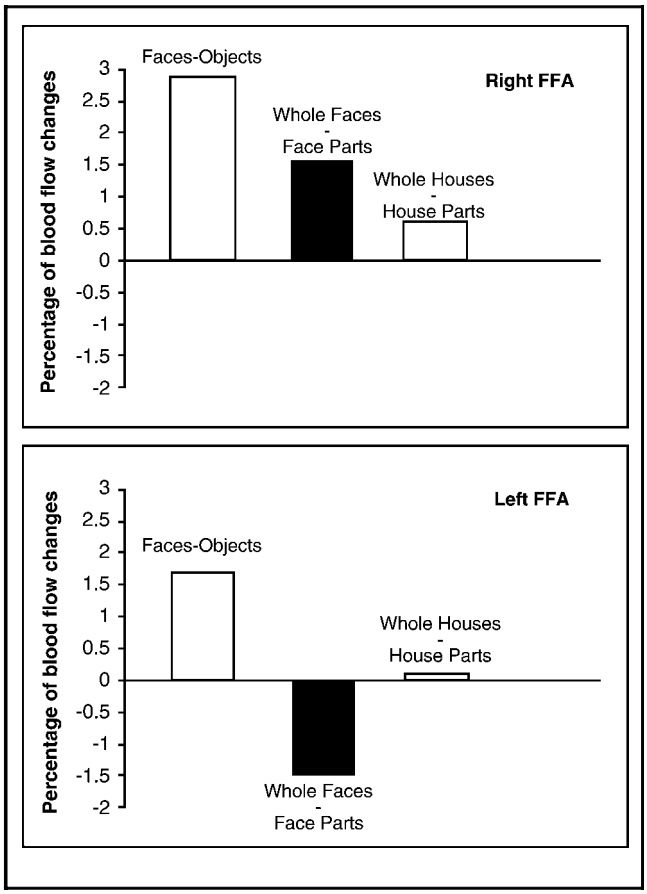

Figure 3. Corrected rCBF group values observed for the six face and object conditions of the study in a spherical region of 3-mm radius (19 voxels) centered on the maxima of the left fusiform face-specific area (lFFA) and on the maxima of the right FFA (left and right, respectively).

– 26 as center was 1.51% (1.53% for voxel – 42, – 50, – 26), indicating that the lFFA was more involved in whole-face processing than in processing of face parts.[4] Again, this effect was specific to faces as no difference between HP and HW was observed within this region (see Figure 3). Within the LO, no reliable difference in brain activity between FW and FP was observed.

DISCUSSION

The study identified three regions of the fusiform gyrus that are face-selective. The right fusiform posterior region was insensitive to whole- or part-based processing of faces. In line with previous discussion regarding these two modes of processing (see Bruce & Humphreys, 1993; Farah, Tanaka, & Drain, 1995), we consider that face parts are not (or less) separately processed in the first case whereas they must be so in the second case. If matching of the whole face is the "normal" strategy, we may argue that face-specific activity is reduced in the right middle fusiform face area when the attention is focused on face components, but it is enhanced in the left hemisphere homologous region. More importantly, these effects are not observed for objects. These different points are successively discussed. The results of the present study have important implications for understanding the role of the different regions of the fusiform gyrus as well as the respective contributions of the two hemispheres in face processing in humans.

Bilateral Regions of the Middle Fusiform Gyrus Are Face-Selective

The data confirm that in humans face processing takes place in the fusiform gyrus with a general right-hemisphere advantage (Dubois et al., 1999; Kanwisher et al., 1997; McCarthy et al., 1997; Sergent et al., 1992). The middle fusiform gyrus is more activated on both sides for faces than objects whereas the posterior fusiform activation was observed only in the right hemisphere. This observation is consistent with previous PET studies (Kapur, Friston, Young, Frith, & Frackowiak, 1995; Haxby et al., 1994; Haxby et al., 1996) that reported bilateral middle and posterior fusiform activations for face processing. However, the recruitment of the left posterior fusiform region for face processing is less often observed (e.g., Dubois et al., 1999). When faces are compared to complex objects there is no evidence of a left posterior fusiform activation (Gauthier et al., 1999b; Kanwisher et al., 1997; McCarthy et al., 1997; the present study), except in two recent fMRI studies (Halgren et al., 1999; Haxby et al., 1999). In contrast, activation of the right posterior fusiform gyrus, or in the right LO (Malach et al., 1995), is regularly observed when faces are compared to various categories of visual objects (Halgren et al., 1999; Haxby et al., 1999; Kanwisher et al., 1997 for four subjects). In addition, such comparisons always give rise to face-specific bilateral activations of the middle fusiform gyrus. The role of these different areas in face processing remains unclear, although our knowledge of the middle right fusiform area has recently increased. Among other findings, it has been shown that activity within this region can be modulated by voluntary attention (Wojciulik, Kanwisher, & Driver, 1998) and may be recruited for non-face objects if the observer has developed a visual expertise with these objects (Gauthier et al., 1999a, 1999b). The present observations strongly support the view that mechanisms specifically dedicated to face processing take place in neural regions located in the human middle fusiform gyrus of *both* hemispheres. Most of the previous neuroimaging studies (Dubois et al., 1999; Gauthier et al., 1999a, 1999b; Halgren et al., 1999; Ishai et al., 1999; Puce et al., 1995; Haxby et al., 1994, 1999) have arrived at the same conclusions. However, the involvement of the left middle fusiform gyrus has been somewhat minimized since its activation is drastically reduced when faces are presented simultaneously with objects (McCarthy et al.,

1997) or when only regions activated in a large subset of subjects, at a very conservative statistical threshold, are considered (Kanwisher et al., 1997). These two previous studies have used passive stimulation paradigms or matching tasks in which subjects may have relied more on configural mechanisms to process faces. In these normal conditions, the face-selective response is larger in the rFFA than in the lFFA, as in the present study (see Figure 3, faces–objects). Thus, depending on task instructions, intersubject variability[5] or statistical criterion, one may either conclude that *only* the rFFA is strictly face-specific (Kanwisher et al., 1997; McCarthy et al., 1997), or that *both* middle fusiform areas are face-selective. By manipulating the subjects' instructions, our study is the first to show that face-selective activity can even be higher in the lFFA than in the rFFA if subjects focus their attention on particular features of the faces.[6] In light of these and previous observations by others (Dubois et al., 1999; Gauthier et al., 1999a, 1999b; Halgren et al., 1999; Ishai et al., 1999; Puce et al., 1995; Haxby et al., 1994, 1999), the claim of a right hemisphere specifically dedicated to faces versus a left hemisphere supporting a more general object-recognition system is questioned.

Part-Based Processing Reduces Face-Specific Activity in the Right-Middle Fusiform Gyrus

The functional significance of the rFFA remain(s) largely unclear (Tovée, 1998). However, recent evidence suggests that face processing in this region can be modulated by voluntary attention (Wojciulik et al., 1998). Another recent fMRI study has also demonstrated that subordinate level categorization, as compared to basic level categorization, may enhance activity in the rFFA for non-face stimuli (Gauthier, et al., in press). In these two latter studies, modulations of brain activity were due to task demands since the stimuli remain identical in the conditions compared. Apart from their relevance to the question of face modularity, these studies show that the rFFA cannot be considered as an automatic recognition system whose activity depends only on stimuli characteristics. In the present study, we provide a third instance of task modulations in the rFFA: face-selective activity is reduced when subjects are instructed to focus their attention on particular features of the faces. This finding is in agreement with our starting hypothesis, which was based on the fact that the right hemisphere advantage for faces crucially depends on face configural mechanisms (Rhodes, 1993). Accordingly, tachistoscopic studies have observed a reduction of the right hemisphere advantage for processing faces when configural analysis of the face is disrupted, either by instructions to match a single feature (Hillger & Koenig, 1991) or by face inversion (Hillger & Koenig, 1991; Levine et al., 1988; Leehey et al., 1978). According to these observations, we might expect the effects of face inversion on brain activity in the rFFA to match closely the patterns we observed here, but the situation turns out to be more complex. While two recent fMRI studies found no effect of inversion upon the magnitude of response in the rFFA (Aguirre, Singh, & D'Esposito, 1999; Haxby et al., 1999), others observed either a small (Kanwisher, Tong, & Nakayama, 1998) or a significant reduction for inverted faces (Gauthier et al., 1999a, Gauthier et al., 1999b). Recordings of human ERPs on the scalp (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Jeffreys, 1993) or from single neurons in the superior temporal sulcus of monkeys (Perrett et al., 1988) did not find any amplitude reduction for inverted faces.[7] Intracranial ERP recordings in humans indicate that both fusiform gyri are almost as sensitive to inverted as to upright faces (McCarthy, Puce, Belger, & Allison, 1999) although the right hemisphere does show a more rapid response to the upright faces and the left hemisphere tends to respond faster to the inverted faces. These temporal differences are in the order of tens of milliseconds and could not be discriminated by PET and fMRI. Rather, intracranial ERP observations (McCarthy et al., 1999; see also Allison, Puce, Spencer, & McCarthy, 1999 and Puce, Allison, & McCarthy, 1999) would suggest that the fMRI signal would be comparable in both hemispheres for inverted and normal faces. However, it may well be that forcing subjects to attend to particular face features to achieve their matching task is a more powerful method to evidence right-left differences in face processing than comparing upright and inverted faces. In line with this suggestion, Hillger and Koenig (1991) observed that the right-hemisphere advantage for face processing disappeared with inversion, but that a left-hemisphere advantage occurs when, in a divided visual field presentation, subjects have to match faces on a single feature.

Face-Specific Activity of the Left Middle Fusiform Gyrus Is Enhanced by Part-Based Processing

Few evidences of a left hemisphere advantage in face processing, especially with unfamiliar stimuli (see Rhodes, 1985), have been reported. A left hemisphere advantage for face processing has been observed in behavioral experiments either when subjects have to search for a single difference (Patterson & Bradshaw, 1975) or similarity (Hillger & Koenig, 1991, experiment 4) between two faces, or to attend to a specified feature of the face (Bradshaw & Sherlock, 1982). In our PET study, we used the latter kind of task with central-stimulus presentation and we observed an increase of brain activity in a face-selective region of the left middle fusiform gyrus. It is the first report of a localized left-hemisphere advantage for face processing. The larger involvement of the left hemisphere in part-based processing is not only supported by face-processing studies (Corballis, 1991). Localized hemispheric asymmetries for identical hierarchical stimuli processed either at the

global or local level have been previously observed in PET and fMRI studies (Martinez et al., 1997; Fink et al., 1996, Fink, Marshall, et al., 1997). Usually, an RH versus LH advantage is found when hierarchical stimuli are processed at the global versus local level, although the effect may strongly depend on the visual category used (Fink, Halligan, et al., 1997). However, it is difficult to relate these observations directly to ours, since a global and local dissociation on hierarchical stimuli is not equivalent to whole-based and part-based processing of faces. In the present study, we paid attention to such task modulations in a limited set of brain areas that were shown to respond more to faces than objects. There was no evidence of a left-middle fusiform advantage for the objects used (houses), although behavioral studies indicating left-hemisphere advantage in analytical tasks for objects (e.g., Bradshaw & Sherlock, 1982) would suggest that such effects may occur in other brain regions. A recent behavioral study has also provided evidence that objects like houses could be processed holistically (Donnelly & Davidoff, 1999). However, we found no advantage of processing whole faces over face parts in our tasks (see behavioral results) which, again, differ from this latter study because we *imposed* the different modes of processing to our subjects.

The exact mechanisms by which these increases and decreases of activity arise in the middle fusiform gyrus are still unclear. Neurophysiological recordings in monkey's inferotemporal lobe have observed differentiable responses to face parts and whole faces (Perrett, Rolss, & Caan, 1982) but there is no evidence of any difference in these responses across hemispheres. The recent data from McCarthy et al. (1999) clearly indicate that such responses exist in humans also, and they are not differentiable across hemispheres. These modulations may also be the result of top-down modulations from temporo-parietal regions to extrastriate areas, as proposed for global/local modulations (Fink, Halligan, et al., 1997). Such top-down modulations have previously been observed for low-level visual features such a color, shape, or movement (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990) in early extrastriate cortex as a result of selective attentional enhancement of functionally specialized neuronal responses (Hillyard, Vogel, & Luck, 1998).

In conclusion, we have shown that the right fusiform face area (rFFA) responds more strongly during processing of whole faces (but not houses) whereas the left fusiform face area (lFFA) is more activated during the imposed processing of parts presented in complete faces. It is the first report from neuroimaging about functional differences in the activation of the left and right FFAs. Recent observations from fMRI studies suggest that extensive artificial (Gauthier et al., 1999b) or natural (Gauthier et al., 1999a) visual expertise with objects may be sufficient to trigger activity comparable to that for faces in the right middle fusiform face area. As these objects can be processed both at the level of individual features or as whole objects (Gauthier & Tarr, 1997), further studies should now test whether the task dissociations evidenced in the present study could occur for such visual objects or whether they truly reflect hemispheric specialization specific to faces.

METHODS

Subjects

Eight right-handed male subjects (age range 22–25 years) provided written consent according to institutional guidelines.

Stimuli

Stimuli used in the control scans were taken from a previous fMRI study (Gauthier et al., 1999b) in which they were used to identify the fusiform face area. Sixteen different faces and 16 different houses were used to make the experimental stimuli (see Figure 1 for a sample of each stimulus category). All stimuli were gray-scale photographic-quality images of faces and houses in frontal view. Images of houses were 7.5 cm wide and 5.5 cm high, and faces were 7.5 cm high and 5.5 cm wide. The actual stimuli were constructed as follows. A prototypical stimulus of each category was selected to serve as a framework providing outline and external features (chin, head, ears for faces; outline, roof, and chimney for houses). In this framework, different components taken from other pictures were inserted to make different faces and houses. Stimuli were presented on a Macintosh AV17 screen (black background) at 120-cm distance.

Tasks

Subjects performed the same delayed-matching task throughout the experiment, either with control objects or control faces, or with houses or faces. Control scans were presented at the beginning (first and second scans) and the end (eleventh and twelfth scans) of the experiment and counterbalanced across subjects. Their aim was to help identify face-specific regions and to minimize the possibility of identifying non-face-specific regions in the localizer contrast, due to particular differences between faces and houses. The block order of faces and houses conditions was counterbalanced for all subjects. The beginning of each trial was signaled by a small white cross that remained on the center of the black screen for 200 msec. Then, a black screen was displayed for 250 msec, followed by a probe stimulus presented in the center of the screen for 1,000 msec. Following the probe stimulus, a black screen was shown for 500 msec before the target stimulus presented for 1,000 msec. The intertrial interval was set at 1,600 msec (black screen) and responses were recorded up to 1,800

msec following onset of the target stimulus. The rather long presentation time of our stimuli (1,000 msec) was chosen, following pilot experiments, to achieve a good level of performance during PET scanning. Even if one cannot exclude that subjects have fixated different aspects for faces and houses in the different tasks with such duration, stimuli were presented foveally so that retinal stimulation should have been roughly equivalent in the different conditions. Twenty-four pairs of trials were presented during a scan. Before each scan, a block of 12 trials with stimuli not shown in the experiment was presented to the subjects. In the processing of whole faces (FW) or houses (HW), the subject was asked to select the right or left key-press of the response box, according to whether the target stimulus was identical or different than the probe stimulus, respectively. On each trial all features were different. In the part-based processing condition (FP), subjects were instructed to push the right or left key on the response box, depending on whether the eyes (one scan) or the mouth (other scan) in the probe face was identical or different than the same feature in the target face. In the part-based condition with houses (HP), subjects were instructed to press either one of the two keys depending on whether the large window (one scan) or the window on the roof (other scan) in the probe stimulus was identical to or different from the same component in the target stimulus. Responses were made with the right hand. To ensure that subjects focused on the critical feature, pairs were constructed such that in the ''same'' trials (12/24), only the critical feature was identical between the probe and the target stimulus. In the ''different'' trials, all features differed in half of the trials (6/12) whereas in the other half of the trials the other features of the stimulus were identical in the probe and the target.

Data Acquisition

Error rates and RTs were collected for each condition and subject. PET data were acquired with an ECAT EXACT-HR 3-D PET tomograph (CTI/Siemens). Each subject was scanned twice in each condition and received intravenous $H_2{}^{15}O$ (8 mCi, 2.96 e + 02 MBq, 20 sec bolus) 10 sec before starting the task. Measurements of local-radioactivity uptake were made with septa retracted. Images were reconstructed with an effective resolution of 8 mm full width at half maximum (FWHM), using filtered back-projection scatter correction, with both transaxial Hanning filter (cutoff frequency of 0.30) and axial Hanning filter (cutoff frequency of 0.50). A two-dimensional transmission scan was acquired for attenuation correction. The task started 10 sec after initiation of tracer injection and PET data were acquired simultaneously in a single 100-sec frame. The integrated counts accumulated during 100-sec scans were used as an index of regional cerebral blood flow (rCBF) (Mazziotta & Phelps, 1986). The time interval between successive emission scans was 13 min, which allowed decay of residual radioactivity. For each subject, 3-D MRI (T1) anatomical data were also obtained on a 1.5-T unit (General Electric Signa).

Data Analysis

PET images were realigned to the first one using AIR (Woods, Cherry, & Mazziotta, 1992) and coregistered to the MRI. They were then spatially normalized (SPM96—Wellcome Department of Cognitive Neurology) to fit the Talairach and Tournoux (1988) coordinate system (voxel size 2 × 2 × 4 mm). Finally, the images were smoothed with a Gaussian filter (15 mm FWHM) and corrected for global activity by proportional scaling (Fox, Mintun, Reiman, & Raichle, 1988). Group statistical maps were made using the general linear model (Friston et al., 1995). Main effects and interactions were assessed with different contrasts using t statistics subsequently transformed into normally distributed Z scores. The face-specific regions were identified ($Z > 3.09$; $p < .001$, uncorrected for multiple comparisons) by comparing all scans performed on faces to all scans performed on objects, including control objects and houses. In a second stage, the main effect of stimulus was used as a mask to test for task modulations within the face-specific regions.

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Notes

1. The term *configuration* refers here to the spatial relations between different parts of the face. These spatial relations are particularly important to discriminate individual faces (see Rhodes, 1993).
2. A small focus of activity was also observed in the right postcental gyrus in the main contrast effect of the group analysis but the pattern of brain activity over the different conditions in this region was not consistent across subjects and its location is out of the concern of this study.
3. By using the term ''double dissociation,'' we do not mean that the rFFA is only involved in some kind of configural face processing while the lFFA would support a part-based processing of faces. Our data indicate that *both* areas are specifically involved in face processing, regardless of task instructions. However, we show that task demands can further

modulate the pattern of face-specific activity in an *opposite* fashion in two different areas.

4. It is worth noting that these increases of activity were not small since the increase of rCBF between faces and objects for the control scans with face and object photographs was 2.85% and 1.67%, respectively, in the rFFA and lFFA, the two regions which have been found to be selectively engaged in face processing by the PET and fMRI studies cited in the text.

5. It is worth noting that in the original study that defined the (r)FFA (Kanwisher et al., 1997), a significant activation of the lFFA was observed in 7 subjects out of 12, including the two left-handed subjects. One of these two subjects did not present a significant stronger response for faces than for objects in the rFFA.

6. The comparison *part-based processing of faces–part-based processing of houses* gave rise to an increase of 3.35% in the lFFA and 2.08% in the rFFA. For the processing based on the whole picture, these differences (faces–houses) were 3.1% in the rFFA and 1.76% in the lFFA.

7. Rather, inverted faces may even enhance face-sensitive components in occipito-temporal regions, at least in active discrimination tasks (Rossion et al., 1999).

REFERENCES

Aguirre, G. K., Singh, R., & D'Esposito, M. (1999). Stimulus inversion and the responses of face and object-sensitive cortical areas. *NeuroReport, 10,* 189–194.

Allison, T., Puce, A., Spencer, D. D., & McCarthy, G. (1999). Electrophysiological studies of human face perception: Potentials generated in occipitotemporal cortex by face and non-face stimuli. *Cerebral Cortex, 9,* 415–430.

Bentin, S., Allison, T., Puce, A., Perez, A., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience, 8,* 551–565.

Bradshaw, J. L., & Sherlock, D. (1982). Bugs and faces in the two visual fields: The analytic/holistic processing dichotomy and task sequencing. *Cortex, 18,* 211–226.

Clark, V. P., Keil, K., Maisog, J. M., Courtney, S., Ungerleider, L. G., & Haxby, J. V. (1996). Functional magnetic resonance imaging of human visual cortex during face matching: A comparison with positron emission tomography. *Neuroimage, 4,* 1–15.

Clark, V. P., Maisog, J. M., & Haxby, J. V. (1998). fMRI study of face perception and memory using random stimulus sequences. *Journal of Neurophysiology, 79,* 3257–3265.

Corballis, M. (1991). *The lopsided ape: Evolution of the generative mind*. New York: Oxford University Press.

Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G., & Petersen, S. E. (1990). Attentional modulation of neural processing of shape, color, and velocity in humans. *Science, 248,* 1556–1559.

De Gelder, B., & Rouw, R. (in press). Configural processing of faces in prosopagnosia. *Cognitive Neuropsychology*.

De Renzi, E. (1986). Prosopagnosia in two patients with CT-scan evidence of damage confined to the right hemisphere. *Neuropsychologia, 24,* 385–389.

Donnelly, N., & Davidoff, J. (1999). The mental representation of faces and houses: Issues concerning parts and wholes. *Visual Cognition, 6,* 319–343.

Dubois, S., Rossion, B., Schiltz, C., Bodart, J.-M., Michel, C., Bruyer, R., & Crommelinck, M. (1999). Effect of familiarity on the processing of human faces. *Neuroimage, 9,* 278–289.

Ettlin, T. M., Beckson, M., Benson, D. F., Langfitt, J. T., Amos, E. C., & Pineda, G. S. (1992). Prosopagnosia: A bihemispheric disorder. *Cortex, 28,* 129–134.

Farah, M. J. (1990). *Visual agnosia: Disorders of object recognition and what they tell us about normal vision*. Cambridge: MIT Press.

Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1996). Where in the brain does visual attention select the forest and the trees? *Nature, 382,* 626–628.

Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1997). Neural mechanisms involved in the processing of global and local aspects of hierarchically organized visual stimuli. *Brain, 120,* 1779–1791.

Fink, G. R., Marshall, J. C., Halligan, P. W., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1997). Hemispheric specialization for global and local processing: The effect of stimulus category. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 264,* 487–494.

Fox, P. T., Mintun, M. A., Reiman, E. M., & Raichle, M. E. (1988). Enhanced detection of focal brain response using intersubject averaging and change-distribution analysis of subtracted PET images. *Journal of Cerebral Blood Flow and Metabolism, 8,* 642–653.

Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J.-P., Frith, C. D., & Frackowiak, R. S. J. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping, 2,* 189–210.

Gauthier, I., & Tarr, M. J. (1997). Becoming a "greeble" expert: Exploring the face-recognition mechanism. *Vision Research, 37,* 1673–1682.

Gauthier, I., Kanwisher, N., Anderson, A., Skudlarski, P., & Gore, J. C. (1999a). Expertise for cars and birds recruits middle fusiform face-selective areas. *Society for Neuroscience Abstracts, 25,* 530.

Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999b). Activation of the middle fusiform area increases with expertise in recognizing novel objects. *Nature Neuroscience, 6,* 568–573.

Gauthier, I., Tarr, M. J., Moylan, J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (in press). Does visual subordinate-level categorization engage the functionally defined fusiform face area? *Cognitive Neuropsychology*.

George, N., Dolan, R. J., Fink, G. R., Baylis, G. C., Russell, C., & Driver, J. (1999). Contrast polarity and face recognition in the human fusiform gyrus. *Nature Neuroscience, 6,* 574–580.

Grill-Spector, K., Kushnir, T., Hendler, T., Edelman, S., Itzchak, Y., & Malach, R. (1998). A sequence of object-processing stages revealed by fMRI in the human occipital lobe. *Human Brain Mapping, 6,* 316–328.

Halgren, E., Dale, A. M., Sereno, M. I., Tootell, R. B. H., Marinkovic, K., & Rosen, B. (1999). Location of human face-selective cortex with respect to retinotopic areas. *Human Brain Mapping, 7,* 29–37.

Haxby, J. V., Horwitz, B., Ungerleider, L. G., Maisog, J. M., Pietrini, P., & Grady, C. L. (1994). The functional organization of human extrastriate cortex: A PET-rCBF study of selective attention to faces and locations. *Journal of Neuroscience, 14,* 6336–6353.

Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., & Martin, A. (1999). The effect of face inversion on activity in human neural systems for face and object perception. *Neuron, 22,* 189–199.

Haxby, J. V., Ungerleider, L. G., Horwitz, B., Maisog, J. M., Rapoport, S. I., & Grady, C. L. (1996). Face encoding and recognition in the human brain. *Proceedings of the National Academy of Sciences, U.S.A., 93,* 922–927.

Hillger, L. A., & Koenig, O. (1991). Separable mechanisms in face processing: Evidence from hemispheric specialization. *Journal of Cognitive Neuroscience, 3,* 42–58.

Hillyard, S. A., Vogel, E. K., & Luck, S. J. (1998). Sensory gain control (amplification) as a mechanism of selective attention: Electrophysiological and neuroimaging evidence. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 353,* 1257–1270.

Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences, U.S.A., 96,* 9379–9384.

Jeffreys, A. D. (1993). The influence of stimulus orientation on the vertex scalp positive potential evoked by faces. *Experimental Brain Research, 96,* 163–172.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience, 17,* 402–4311.

Kanwisher, N., Tong, F., & Nakayama, K. (1998). The effect of face inversion on the human fusiform face area. *Cognition, 68,* B1–B11.

Kapur, N., Friston, K. J., Young, A., Frith, C. D., & Frackowiak, R. S. J. (1995). Activation of human hippocampal formation during memory for faces: A PET study. *Cortex, 31,* 99–108.

Landis, T., Regard, M., Bliestle, A., & Kleihues, P. (1988). Prosopagnosia and agnosia from noncanonical views. An autopsied case. *Brain, 11,* 1287–1297.

Leehey, S. C., Carey, S., Diamond, R., & Cahn, A. (1978). Upright and inverted faces: The right hemisphere knows the difference. *Cortex, 14,* 414–419.

Levine, S. C., Banich, M. T., & Koch-Weser, M. P. (1988). Face recognition: A general or specific right hemisphere capacity? *Brain and Cognition, 8,* 303–325.

Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., Ledden, P.J., Brady, T. J., Rosen, B. R., & Tootell, B. H. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences, U.S.A.,* 8135–8139.

Martinez, A., Moses, P., Frank, L., Buxton, R., Wong, E., & Stiles, J. (1997). Hemispheric asymmetries in global and local processing: Evidence from fMRI. *NeuroReport, 8,* 1685–1689.

Mazziotta, J. C., & Phelps, M. E. (1986). Positron emission tomography studies of the brain. In M. E. Phelps, J. Mazziotta & H. Schelbert (Eds.), *Positron emission tomography and autoradiography: Principles and applications for the brain and heart* (pp. 493–579). New York: Raven Press.

McCarthy, G., Puce, A., Belger, A., & Allison, T. (1999). Electrophysiological studies of human face perception: Response properties of face-specific potentials generated in occipitotemporal cortex. *Cerebral Cortex, 9,* 431–444.

McCarthy, G., Puce, A., Gore, J. C., & Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience,9,*605–610.

Michel, F., Poncet, M., & Signoret, J.-L. (1989). Les lésions responsables de la prosopagnosie — sont elles toujours bilatérales? *Revue Neurologique, 145,* 764–770.

Moscovitch, M., Winocur, G., & Behrmann, M. (1997). What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience, 9,* 555–604.

Patterson, K., & Bradshaw, J. L. (1975). Differential hemispheric mediation of nonverbal visual stimuli. *Journal of Experimental Psychology: Human Perception and Performance, 3,* 246–252.

Perrett, D. I., Mistlin, A. J., Chitty, A. J., Smith, P. A. J., Potter, D. D., Broennimann, R., & Harries, M. (1988). Specialized face processing and hemispheric asymmetry in man and monkey: Evidence from single unit and reaction times studies. *Behavioral Brain Research, 29,* 245–258.

Perrett, D. I., Rolls, E. T., & Caan, W. (1982).Visual neurons responsive to faces in the monkey temporal cortex. *Experimental Brain Research, 47,* 329–342.

Puce, A., Allison, T., Gore, J. C., & McCarthy, G. (1995). Face-sensitive regions in human extrastriate cortex studied by functional MRI. *Journal of Neurophysiology, 74,* 1192–1199.

Puce, A., Allison, T., & McCarthy, G. (1999). Electrophysiological studies of human face perception: Effects of top-down processing on face-specific potentials. *Cerebral Cortex, 9,* 445–458.

Rhodes, G. (1985). Lateralized processes in face recognition. *British Journal of Psychology, 76,* 249–271.

Rhodes, G. (1993). Configural coding, expertise, and the right hemisphere advantage for face recognition. *Brain and Cognition, 22,* 19–41.

Rhodes, G., Brake, S., & Atkinson, A. P. (1993). What's lost in inverted faces? *Cognition, 47,* 25–57.

Rossion, B., Delvenne, J. F., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., & Guérit, J.-M. (1999). Spatio-temporal localization of the face inversion effect: An event-related potentials study. *Biological Psychology, 50,* 173–189.

Sergent, J., Otha, S., & McDonald, B. (1992). Functional neuroanatomy of face and object processing: A positron emission tomography study. *Brain, 115,* 15–36.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.

Tanaka, J., & Farah, M. J. (1993). Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology, 46A,* 225–245.

Tovée, M. J. (1998). Face processing: Getting by with a little help from its friends. *Current Biology, 8,* R17–R320.

Wojciulik, E., Kanwisher, N., & Driver, J. (1998). Covert visual attention modulates face-specific activity in the human fusiform gyrus: fMRI study. *Journal of Neurophysiology, 79,* 1574–1578.

Woods, R. P., Cherry, S. R., & Mazziotta, J. C. (1992). Rapid automated algorithm for aligning and reslicing PET images. *Journal of Computer-Assisted Tomography, 16,* 620–633.

Yin, R. K. (1970). Face recognition by brain-injured patients: A dissociable ability? *Neuropsychologia, 8,* 395–402.